

Radiotelemetric Analysis of the Effects of Prevailing Wind Direction on Mormon Cricket Migratory Band Movement

G. A. SWORD,^{1,2} P. D. LORCH,^{1,3} AND D. T. GWYNNE^{1,4}

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ABSTRACT During outbreaks, flightless Mormon crickets [*Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae)] form large mobile groups known as migratory bands. These bands can contain millions of individuals that march *en masse* across the landscape. The role of environmental cues in influencing the movement direction of migratory bands is poorly understood and has been the subject of little empirical study. We examined the effect of wind direction on Mormon cricket migratory band movement direction by monitoring the local weather conditions and daily movement patterns of individual insects traveling in bands over the same time course at three close, but spatially distinct sites. Although weather conditions were relatively homogeneous across sites, wind directions tended to be more variable across sites during the morning hours, the period during which directional movement begins. Migratory bands at different sites traveled in distinctly different directions. However, we failed to find any evidence to suggest that the observed variation in migratory band movement direction was correlated with local wind direction at any time during the day. These results support the notion that the cues mediating migratory band directionality are likely to be group specific and that a role for landscape-scale environmental cues such as wind direction is unlikely.

KEY WORDS *Anabrus simplex*, katydid, collective movement, radiotransmitter, hopper band

Mormon crickets [*Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae)] as well as juvenile locust hoppers (Orthoptera: Acrididae) are flightless and, during outbreaks, they form large mobile groups called migratory bands in which millions of individuals march *en masse* across the landscape. Mormon cricket bands can be up to 12 km long, several kilometers wide, and travel up to 2 km/d (Cowan 1929, Wakeland 1959, MacVean 1987, Gwynne 2001, Lorch et al. 2005). The formation of these mobile groups has been causally linked to protection from predators. Insects within migratory bands are much less likely to be killed by predators relative to individuals separated from the band (Sword et al. 2005).

Once bands have formed, the mass movement of Mormon crickets seems to be caused by the combined effects of resource deprivation and cannibalism. Individuals within bands have been shown to be both protein and salt deprived. As a result of nutritional

deprivation, individuals walk more to encounter new resources and also resort to cannibalism to redress their nutritional imbalances (Simpson et al. 2006). Band members that fail to move quickly fall victim to conspecific cannibals approaching from the rear, thereby providing a novel push from behind mechanism that promotes constant directional movement of individuals within the band (Simpson et al. 2006). Behavioral interactions among individual Mormon crickets at high population density are known to play an important role in the induction of their movement (Sword 2005) and likely serve as the mechanism by which the collective movement patterns of individuals in migratory bands arise at high population densities (Couzin and Krause 2003, Buhl et al. 2006).

Empirical evidence suggests that Mormon crickets often are not a major threat to rangeland forage plants in their native range of western North America (Ueckert and Hansen 1970, Redak et al. 1992, MacVean 1987, 1990, Simpson et al. 2006). However, the movement of migratory bands into agricultural systems can result in swift and severe damage to crops (Cowan 1929, Swain 1944, Wakeland 1959). Mormon crickets may also pose a threat to public safety by causing slick, dangerous driving conditions when crushed in large numbers by vehicles as migratory bands cross roadways (Wakeland 1959, Gwynne 2001). Millions of dollars are spent annually to control Mormon crickets during outbreak periods. These expenditures highlight the need for development of new management tools such as predictive movement models that can improve the effi-

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¹ USDA-ARS, Northern Plains Agricultural Research Laboratory, 1500 N. Central Ave., Sidney, MT 59270.

² Corresponding author: School of Biological Sciences, The University of Sydney, Macleay Bldg. A12, Sydney, NSW 2006, Australia (e-mail: greg.sword@bio.usyd.edu.au).

³ Department of Biological Sciences, Kent State University, 256 Cunningham Hall, Kent, OH 44242-0001.

⁴ Department of Biology, University of Toronto at Mississauga, Mississauga, Ontario L5L 1C6, Canada.

ciency and efficacy of control efforts while reducing undesirable nontarget effects.

Radiotelemetry is increasingly being used as a tool in analyses of insect ecology and movement (Cooke et al. 2004; Sword et al. 2005; Wikelski et al. 2006). Because of their relatively large size, individual Mormon crickets can readily be fitted with small radiotransmitters (Lorch and Gwynne 2000), thus providing a tractable model system for understanding the movement patterns of insects that travel in migratory bands. As such, we embarked on a radiotelemetry-based examination of the mechanisms underlying the landscape-scale movement of migratory bands to determine if their movement patterns can be predicted (Lorch et al. 2005). The examination of environmental cues affecting migratory band movement patterns is an important precursor to the development of predictive movement models (Turchin 1998), and also has implications for the understanding of collective animal movement patterns in general (Couzin and Krause 2003).

To date, few empirical studies have examined the environmental cues that may influence the movements of Mormon cricket migratory bands (MacVean 1987, Lorch et al. 2005). Wind direction is one obvious landscape-scale environmental cue detectable by all group members that could feasibly result in group movement via individual anemotaxis. Wind is known to play a major role in the direction of flying locust swarms, with individuals flying downwind to regions where different air masses may collide and potentially generate rainfall (Farrow 1990, Deveson et al. 2005). Such a response to wind direction as an adaptation for finding areas that have received rainfall seems unlikely for flightless insects in migratory bands that travel much shorter distances on the ground. However, directional movement in response to wind could feasibly serve to reduce the likelihood of band members returning to an area that has been depleted of nutritional resources (see Simpson et al. 2006).

The role of wind direction in locust hopper band movement has received more attention than it has in Mormon crickets, but the evidence for an effect on band directionality is scant and inconclusive (Uvarov 1977). Furthermore, multiple locust bands traveling in different directions in the same region over the same time period have been observed, suggesting little if any effect of a landscape-scale cue such as wind on group direction (Ellis and Ashall 1957). Conclusions regarding the effects of wind direction on Mormon cricket band movement based on the observations of early investigators are equally ambiguous (Cowan 1929, Swain 1944, MacVean 1987). Similar to locust hopper bands, different Mormon cricket bands have also been observed to travel in multiple compass directions in the same vicinity at the same time, leading MacVean (1987) to suspect the presence of band-specific rather than general orientation cues. Using small radiotransmitters, Lorch et al. (2005) conducted the first quantitative analysis of the movement of individual Mormon crickets traveling within migratory bands. Although the study was not designed to directly

examine cues mediating migratory band direction, Lorch et al. (2005) did find some evidence to suggest that band direction might be influenced by daily variation in wind direction, primarily in the early morning hours as these diurnal insects begin to organize and set out in directional group movements (Pfadt 1994).

Here, we examine in greater detail the hypothesis that prevailing wind direction influences the direction of Mormon cricket band movement. We compared the daily movement patterns and local weather conditions experienced by individual Mormon crickets traveling during the same time period within three close, but spatially distinct migratory bands.

Materials and Methods

Study Sites. The Mormon cricket bands examined in this study were located in a relatively small, 126-km² region south of Dinosaur National Monument in northwest Colorado and northeast Utah. Three non-overlapping, spatially distinct migratory bands were examined at different sites referred to here as Stateline (40°26'01" N, 109°02'53" W), Snow (40°24'58" N, 109°02'50" W), and K-Creek (40°21'35" N, 108°57'14" W). The study region is a high desert plateau with locally variable topography, plant community composition, and habitat structure. Vegetation at all sites was dominated by sagebrush, *Artemesia tridentata*. Other common forbs and grasses included *Achillea millefolium*, *Agropyron smithii*, *Amelanchier alnifolia*, *Artemesia nova*, *Astragalus* spp., *Balsamorhiza sagittata*, *Bouteloua gracilis*, *Cercocarpus montanus*, *Gutierrezia sarothrae*, *Juniperus scopulorum*, *Juniperus osteosperma*, *Lupinus* spp., *Opuntia polyacantha*, *Stipa comata*, and *Symphoricarpos occidentalis*. Topography varied from relatively flat areas to hills interspersed with local drainages. Habitat structure varied from shortgrass pastures created by sagebrush removal to areas dominated by larger 1-m sagebrush plants. All of the sites were routinely grazed and contained considerable amounts of bare ground over which the crickets marched. By virtue of their size and movement, a single migratory band can stretch across multiple habitat types, with individual band members potentially encountering several different types of habitat and topography over the course of a single day (Lorch et al. 2005).

Data Collection. The movements of 10 young adult (2–3 g) Mormon crickets (5 male and 5 female) within each of the three migratory bands were tracked concurrently from 10 to 14 June 2004. Individuals were relocated once daily using the protocols described in Lorch et al. (2005). Briefly, 0.45-g Micro-Pip radio-transmitters (Biotrack Ltd., Wareham, United Kingdom) were affixed to individuals with a drop of hot glue on the dorsal surface of the pronotum. Carrying the transmitters has been shown to have no discernible effect on individual movement behavior (Lorch et al. 2005). Insects were initially captured, tagged, and released at 10-m intervals along a transect perpendicular to the perceived direction of band movement. Tagged individuals were relocated daily on foot using

a LA12-Q radio receiver and a hand-held Yagi directional antenna (AVM Instrument Co., Colfax, CA). The release position and time as well as all subsequent relocation events were recorded using a submeter accurate Trimble TSC1 Asset Surveyor DGPS System. Differentially corrected GPS data were exported from Pathfinder Office 2.51 (Trimble Navigation, Sunnyvale, CA) into ArcMap 8.3 (ESRI, Redlands, CA). For each insect, point to point distance and heading from magnetic north were calculated between successive daily recapture intervals. Before tracking, portable weather stations (Vantage Pro Weather Station; Davis Instruments, Hayward, CA) were set up at the initial release sites to record local weather conditions. Temperature and prevailing wind (direction and speed) variables were measured at 1 and 2 m above the ground, respectively. Weather parameters were saved to a data logger at 15-min intervals over the duration of tracking and downloaded to a laptop PC computer.

Analysis. Variation in local daily wind speed and temperature patterns among sites was examined graphically by plotting temperature and wind speed versus time for each site over the tracking duration. Variation in wind direction across sites over time was examined by plotting the consistency of the circular mean wind direction (r) (Zar 1999) across sites binned at hourly intervals. Consistency values were calculated across all sites at 15-min intervals, with four 15-min intervals/h and 5 d of weather data collection resulting in 20 possible r values per hourly bin. Consistency across sites was not calculated when a wind direction value at any site was not recorded because of a wind speed value of 0 km/h. This resulted in a range of $N = 9$ –20 r values per hour. Consistency values range from 0 to 1 as the directedness of a group of angular measurements varies from random to completely consistent. Consistency is used here as a quantitative measure of wind direction heterogeneity across sites over time.

The direction of migratory band movement was quantified by calculating the circular mean direction (Zar 1999) of the 10 individuals within each band over each daily recapture interval, yielding four daily measures of band direction for each of the three bands. Consistency of the daily circular mean band movement direction was calculated and its significance tested with Raleigh's test of uniformity (Zar 1999). Daily distances traveled by individual insects were transformed to daily rates of movement to control for variation in recapture interval. Previous work has shown no difference in either movement rate or direction between the sexes; therefore, sex was ignored in the analyses (Lorch et al. 2005).

To examine the possible influence of wind direction on band direction at certain critical periods during the day (Lorch et al. 2005), we performed 12 circular correlation analyses (Zar 1999) between daily circular mean band direction and circular mean wind direction. These correlations were done at 1-h intervals ranging from 0600 to 1800 hours, a period spanning the primary diurnal marching activity period (Pfadt 1994). Each correlation coefficient represents the correla-

tion between the daily circular mean band movement direction and the circular mean wind direction at that particular 1-h time interval across 4 d at each of the three sites for a maximum of $N = 12$ points. 0600, 0700, and 0800 hours had 5, 5, and 10 points, respectively, because of windspeed readings of zero. The 12 hourly correlation coefficients obtained from these analyses were plotted versus time interval to determine the extent to which wind direction during a particular period during the day could reliably predict band movement direction. If wind direction during a particular period has an important influence on daily band movement direction, we would expect it to have a high correlation relative to other times. A similar analysis was conducted over the whole day by combining all the wind and movement direction data for a given site and day.

Results

Daily weather patterns were relatively homogeneous across all the tracking sites. Skies were clear and no rain fell over the course of the study. Nighttime low temperatures were slightly lower at Snow, and daytime high temperatures tended to be slightly higher at K-Creek. Overall, daytime high temperatures became progressively warmer over the 5-d tracking period (Fig. 1A). Daily fluctuations in wind speed were also homogeneous across sites during the tracking period (Fig. 1B). Within days, wind speeds were lowest at night and early morning and increased sharply by mid-day. Wind direction tended to be more variable across sites than either temperature or wind speed (Fig. 2). Although mean daily wind directions were often similar across sites as well as consistent within sites (Table 1), there were specific periods during daylight hours, particularly in the morning, in which the consistency of wind direction across sites decreased to values of $r < 0.5$, suggesting that wind directions were tending toward random across sites (Fig. 2).

Of the three Mormon cricket bands concurrently tracked, the K-Creek and Snow bands initially traveled along a westerly heading while the Stateline band moved to the east (Fig. 3; Table 1). The movement direction of the Stateline and K-Creek bands in opposite compass directions remained constant across the tracking duration (Fig. 3; Table 1). However, the Snow band bifurcated beginning on 12 June, with some radiotagged individuals within the band adopting a more northerly heading, whereas others continued heading to the west or southwest (Fig. 3).

The bifurcation of the Snow band had the effect of lowering the consistency of band direction values on 12 and 13 June (see Table 1). However, it was apparent from observations on the ground that the radio-tagged insects were moving in two separate groups headed in different directions. Thus, the lower band consistency values within the Snow band on these days do not indicate a lack of directional movement within the band, but rather that the insects had split into two distinct groups with their own unique headings. With

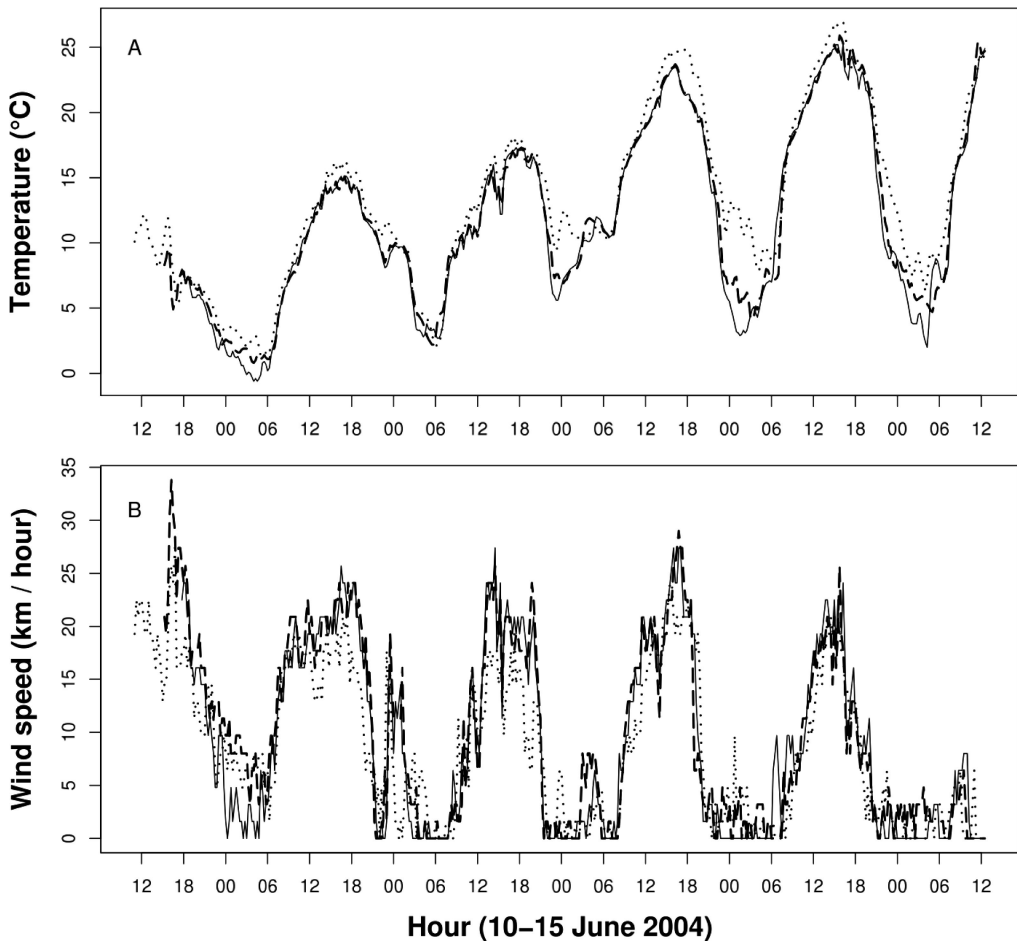


Fig. 1. Daily patterns of temperature and wind speed variation at three spatially distinct migratory band radiotracking sites. Data were recorded at 15-min intervals across the radiotracking period (K-Creek, dotted; Snow, solid; Stateline, dashed). (A) Temperature variation over time. (B) Wind speed variation over time.

the exception of the bifurcation event at the Snow site, band movement at all other sites for the duration of tracking was very directional, with highly significant consistency of band movement values often approaching $r = 1$ (Table 1).

The average daily distance and rate traveled by individuals within bands differed slightly among bands but tended to increase across sites during the tracking period as daytime temperatures increased (Table 1; Figs. 1A and 3). Average individual rates of movement varied from 8.9 to 58.9 m/h corresponding to daily average individual movement distances ranging from 185 to 1,446 m/d. One individual within the K-Creek band was observed to have moved 2,119 m over a single daily tracking interval of 25 h 17 min, the longest daily movement of a Mormon cricket that we have recorded to date (Lorch et al. 2005).

Average daily wind direction and average daily band movement direction were not correlated ($N = 12$, circular $r = 0.067$, test statistic = 0.22, $P = 0.83$), suggesting that variation in wind direction at this time scale does not adequately account for variation in

band movement direction. Because wind directions were more variable across sites at certain periods of the day (Fig. 2), and we observed bands at different sites traveling in different directions (Table 1; Fig. 3), we examined the correlation between circular mean wind and daily band direction at 1-h intervals from 0600 to 1800 hours. Plotting the correlation coefficients over time showed no substantial relationship between wind direction and migratory band travel direction at any point during the sampled intervals (Fig. 4), and none of these correlations were significant.

Discussion

Prevailing wind direction seems to play little if any role in determining the direction of Mormon cricket migratory band movement. Radiotracked individuals traveling in nearby, but spatially distinct, migratory bands exhibited major differences in movement direction, in some cases traveling in opposite compass directions (Fig. 3) even though local wind and tem-

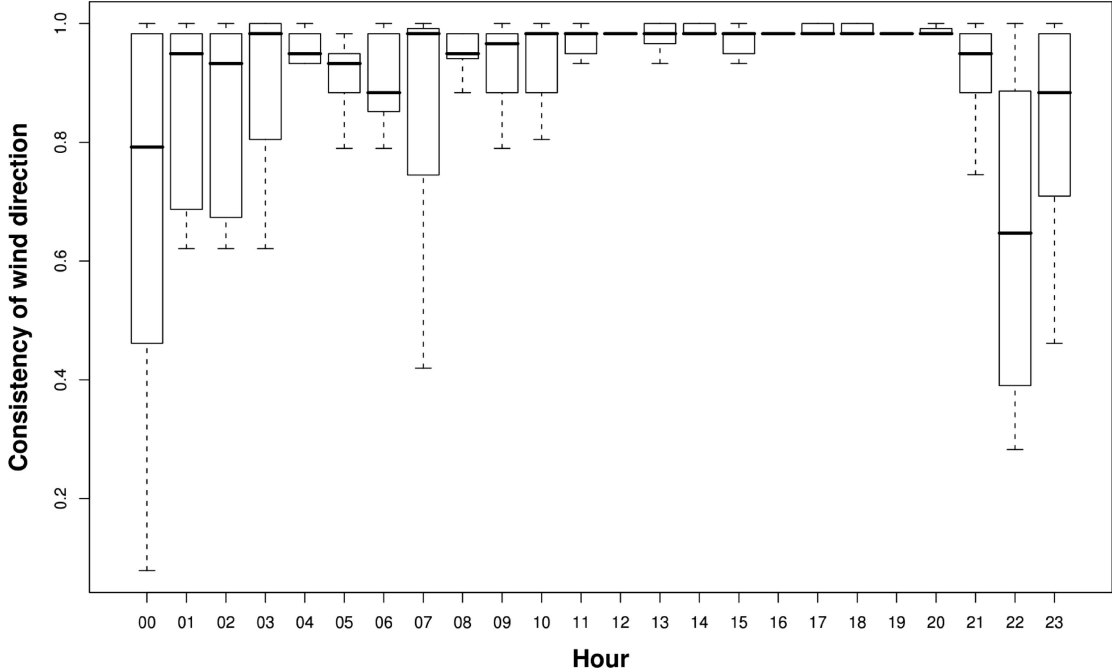


Fig. 2. Box plots depicting the directional consistency (r) of wind directions across three spatially distinct migratory band radiotracking sites plotted in hourly bins. Data were recorded at 15-min intervals at each site across the radiotracking period. Each box displays the median value with the ends of the boxes representing the 25th and 75th percentiles and the ends of the lines representing the 10th and 90th percentile values.

perature regimens were relatively homogeneous across all sites (Figs. 1 and 2). Local wind directions tended to be more variable across sites during the morning hours, potentially providing a means by which variation in band movement directions could arise if local wind direction was being used as a directional cue by Mormon crickets as they begin to organize and move at the beginning of the day (Fig. 2) (Lorch et al. 2005). Despite this possibility, we found no evidence of a correlation between local wind direction and migratory band movement direction during the morning or at any other time during the day

(Fig. 4). Although we sampled both insects and wind direction at each site across consecutive days, any potential nonindependence among the data points should strengthen rather than weaken any observed correlations. Importantly, we observed no significant correlations whatsoever between wind and band directions in this study, suggesting little if any bias caused by nonindependence.

The conclusion that Mormon crickets within migratory bands do not orient with respect to wind direction necessarily rests on the assumption that the prevailing wind direction measured at weather sta-

Table 1. Summary of daily migratory band movement parameters and daily wind directions at each site over the radiotracking duration

Site	Date	N _{wind}	Avg. wind direction (°)	Wind consistency (r)	N _{band}	Avg. band direction (°)	Band consistency (r)	Individual distance (mean ± SE m)	Individual rate (mean ± SE m/h)
K-Creek	6/11/04	96	242	0.858 ^a	10	249	0.971 ^a	214 ± 32	9.7 ± 1.4
	6/12/04	92	241	0.466 ^a	10	255	0.999 ^a	1036 ± 51	43.9 ± 2.0
	6/13/04	92	247	0.519 ^a	10	243	0.999 ^a	1198 ± 36	50.3 ± 1.7
	6/14/04	95	170	0.162	10	253	0.991 ^a	1446 ± 129	58.9 ± 4.8
Snow	6/11/04	94	237	0.843 ^a	10	293	0.970 ^a	328 ± 42	16.7 ± 2.1
	6/12/04	90	254	0.631 ^a	9	292	0.818 ^b	550 ± 36	21.7 ± 1.4
	6/13/04	83	264	0.818 ^a	9	332	0.396	805 ± 67	32.4 ± 2.6
	6/14/04	44	240	0.345 ^a	6	90	0.139	1030 ± 104	36.9 ± 3.8
Stateline	6/11/04	94	243	0.853 ^a	10	73	0.971 ^a	185 ± 29	8.9 ± 1.4
	6/12/04	91	248	0.449 ^a	10	51	0.999 ^a	784 ± 83	31.7 ± 3.3
	6/13/04	92	259	0.523 ^a	10	66	0.995 ^a	1229 ± 63	52.4 ± 2.5
	6/14/04	91	125	0.172	9	73	0.965 ^a	1229 ± 59	47.2 ± 2.5

Average directions were calculated as circular mean directions and converted to degrees for comparison with map in Fig. 3 (0° is north; distance is over roughly 24 h).

^a $P < 0.0001$; ^b $P < 0.001$.

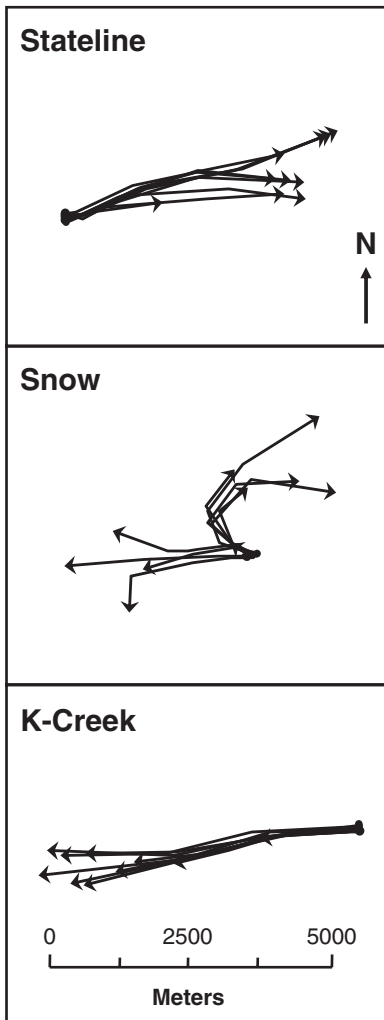


Fig. 3. Movement patterns of individual Mormon crickets traveling in migratory bands at three close, but spatially distinct sites. Insects at all three sites were tracked concurrently from 10 to 14 June 2004. Each line segment depicts 1 d of movement, and the arrowheads indicate the location and heading of the insects at their final sampling point. See Table 1 for distance and direction summary data.

tions 2 m above ground matches that experienced by crickets walking at ground level. Boundary layer effects are known to influence wind speed and, to a lesser extent, direction. Wind speed decreases along a vertical gradient until ultimately reaching zero at the air-ground interface. The vertical distribution of speeds is highly influenced by roughness at the surface generated by objects such as plants and rocks. Similarly, these objects may also influence airflow direction close to the ground at a fine scale relevant to individual insects, particularly at low speeds (Geiger et al. 1995, Vogel 1996). Despite this, we contend that individual band members are repeatedly exposed to prevailing winds by virtue of their spatial distribution across varying topography and habitat structures in

conjunction with their movement through different microhabitats over the course of a day. If local air movements caused by boundary layer effects influence the movement directions of individual crickets, we might expect to observe heterogeneity as opposed to homogeneity in individual movement directions across the band. Despite this potential source of variation in wind directions among locations, individuals tend to travel in a common direction regardless of their position in the band (Fig. 3). Furthermore, the common direction traveled by these individual band members does not seem to be correlated with prevailing wind direction (Fig. 4). Thus, our data fail to suggest an effect of either boundary layer or prevailing wind airflows on migratory band movement direction.

In our analyses, we examined the effect of prevailing wind direction variation on migratory band movement over time rather than as a function of temperature change. Given that insects are exothermic, one could reasonably argue that our use of time as a surrogate for temperature fails to compensate for daily variation in temperature at any given time during the day. However, the spontaneous movement of Mormon crickets in groups does not occur simply on reaching some threshold air temperature. Mormon cricket migrations may start at any time over a broad range of rising air temperatures between 16 and 27°C (Cowan 1990). Also, because of thermoregulatory behavior such as basking in groups in exposed sunlit patches on the ground (Cowan 1929, 1990), individual Mormon crickets' body temperatures are not likely to directly correspond to air temperature. In addition, skies were clear throughout this study removing the potential confound of variation among sites in radiant energy available for basking. For these reasons, we examined the effects of wind direction on band direction versus time as opposed to air temperature, but acknowledge that neither time nor air temperature is likely to correspond perfectly to the behavioral and physiological mechanisms that underlie the initial induction of mass movement.

A summary of previous studies based on field observations came to the same conclusion as our study regarding the lack of a wind direction effect on Mormon cricket migratory band movement (MacVean 1987). Our study provides both quantitative weather and insect movement data to support the earlier conclusion based on qualitative observations that band-specific, as opposed to landscape-scale environmental cues, likely determine the direction that a given migratory band of Mormon crickets will travel. Our data also provide a quantitative demonstration of Mormon cricket bands in the same area traveling in different compass directions (Fig. 3), an observation that further suggests the lack of any landscape-scale environmental cues influencing band movement direction (Ellis and Ashall 1957, Uvarov 1977, MacVean 1987).

Analyses of the movements of individual Mormon crickets traveling in migratory bands have shown their movement patterns to be highly directional at the group level (Fig. 3; Table 1) (Lorch et al. 2005). In the absence of a landscape-scale cue such as wind direc-

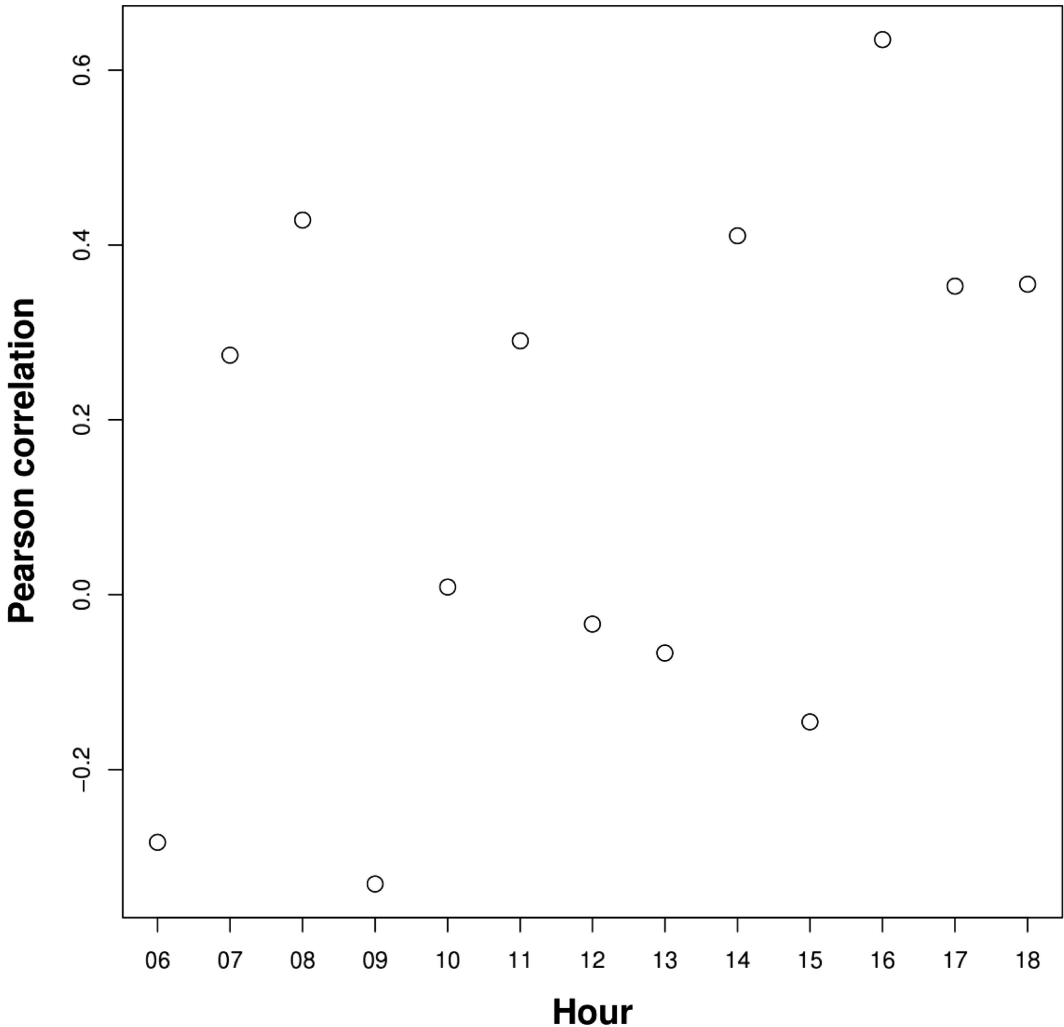


Fig. 4. Circular correlation coefficients indicating the correlation between the daily circular mean of band movement direction and circular mean wind direction for each hour from 0600 to 1800 hours. None of these correlation coefficients were significantly different from zero (all $P > 0.58$), and there was no discernible pattern of higher correlations between band and wind directions at certain parts of the day.

tion that could be detected and responded to by all group members, what can account for these directional group movements? Collective movement models in which animal group movement patterns occur as the result of interactions among individuals following relatively simple underlying behavioral rules have shown that such cues are not needed for directional group movement to arise (Krause and Ruxton 2002, Couzin and Krause 2003). Thus, group movement direction can be an intrinsic property of a self-organizing group of interacting individuals and be determined independently in different groups.

Although our study does not conclusively rule out the possible existence of environmental cues that might influence migratory band direction, our results are much more consistent with the scenario of local self-organization, with movement direction arising as a band-specific property. Mormon crickets are diur-

nal, and migratory bands cease moving at night (MacVean 1987, Pfadt 1994). This cessation of group movement provides the opportunity for group-level properties such as movement direction to be reset, potentially resulting in the group adopting a new heading as organization and movement begin the next day. However, Mormon cricket band movement patterns are not random across days as might be expected if directionality was purely a result of local self-organization. Migratory bands have repeatedly been observed to travel in the same direction over consecutive days (Fig. 3) (Lorch et al. 2005). These observations beg the question of how such a pattern can occur in the absence of landscape-scale cues. Couzin et al. (2005) examined collective movement and information transfer in groups of naïve individuals as it relates to the direction of movement in groups such as bee swarms and fish schools. They found that the propor-

tion of "informed individuals" necessary to generate accurate directional movement patterns actually decreases as group size increases. We suggest that perhaps a very small proportion of Mormon cricket individuals may continue their directional movements at night, effectively acting as informed individuals that can seed band directionality the following day.

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